

Bonn zoological Bulletin	Volume 60	Issue 1	pp. 95–101	Bonn, May 2011
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Revisiting the species status of *Pecari maximus* van Roosmalen et al., 2007 (Mammalia) from the Brazilian Amazon

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Abstract. Three extant species of peccaries (Tayassuidae) are currently recognized and are distributed in the Americas: *Pecari tajacu*, *Tayassu pecari* and *Catagonus wagneri*. The recent claim for a new peccary species, *Pecari maximus*, raises questions about whether there is sufficient molecular or other evidence to support it as a new species. Here, we revisit that evidence using 91 published and 50 novel DNA sequences mainly from *P. tajacu*, as well as comment on the morphological and ecological evidence used to support such a claim. Phylogenetic analyses show that the single specimen of *P. maximus* used clustered within the South American lineage of *P. tajacu* closely related to Brazilian specimens. In addition, the morphological and ecological data used to claim the species status of *P. maximus* appears to be deficient and inconclusive, in the light of available literature.

Key words. Collared peccary, control region, mitochondrial DNA, *Pecari maximus*, *Pecari tajacu*, Tayassuidae.

INTRODUCTION

Three extant species of peccaries (Tayassuidae) are currently recognized: *Pecari tajacu* (Collared peccary), *Tayassu pecari* (White-lipped peccary) and *Catagonus wagneri* (Chacoan peccary) (Wetzel et al. 1975; Woodburne 1968; Wright 1989, 1993). These species have been identified according to morphological and cytogenetic parameters and more recently using DNA sequences. Classification has generally relied on biological concepts of

reproductive and genetic isolation. One confounding factor is that *P. tajacu* and *T. pecari* are known to hybridize in captivity (Sowls 1997) and in the wild with the latter being reproductively sterile (Andrea et al. 2001). Cytogenetic studies have confirmed the existence of three species, showing significant chromosomal differences in number and structure: *P. tajacu* (2n=30), *T. pecari* (2n=26) and *C. wagneri* (2n=20) (Benirschke & Kumamo-

to 1989). Although chromosome painting across species (Bosma et al. 2004) has provided some chromosomal evolutionary insights into this family, a full understanding of the species relationships from a cytogenetic perspective remains hampered by a lack of information on *C. wagneri*. However, phylogenetic analyses of mitochondrial and nuclear DNA sequences have revealed that *T. pecari* and *C. wagneri* grouped in separate clades from *P. tajacu* (Gongora & Moran 2005; Theimer & Keim 1998). These conclusions obtained from molecular markers contrast with cladistic analyses of morphological data which proposed two different scenarios of relationships: First, *P. tajacu* and *C. wagneri* are more closely related whereas *T. pecari* is considered to be a member of a separate clade (Wright 1989, 1993, 1998); and second, *P. tajacu* and *T. pecari* are more closely related to each other than to the *C. wagneri* (Wetzel et al. 1975; Wetzel 1977).

The new species *Pecari maximus*. The recent claim of a new peccary species by van Roosmalen et al. (2007) raises questions about whether there is sufficient molecular and/or other evidence to recognise *P. maximus* as a new species. The morphological and genetic evidence used by van Roosmalen et al. (2007) to support the species status for *P. maximus* appears to be controversial. They analysed a small number of specimens from deceased animals (five skins and three skulls, two of which were from adults), and the body weight (40–50 kg) and size of the animals (total body length 127 cm; ear length 13 cm; shoulder height 85 cm) were estimated from reports and photographs by local hunters. Morphometric analyses were also estimated from skin measurements, and they relied on pelage colour to point the differences with other species. In this study, the mitochondrial control region and two nuclear SINE PRE-1 sequences of a single individual were used to assess the phylogenetic position of *P. maximus* among recognised species of peccaries. In addition, van Roosmalen et al. (2007) used morphological and behavioural data to support a separate status for those peccaries. These authors argue that in contrast with the other peccary species, which they suggest roam semi-nomadically in a highly variable landscape in a noisy herd, *P. maximus* appears to walk silently through its habitat in small family groups that contain a single adult pair with or without 1–2 offspring. They also claim that *P. maximus* performs little or no uprooting and has been seen feeding mainly on freshly fallen fruits and seeds exposed on the forest floor, which appears to be result of direct observations. The claim by van Roosmalen et al. (2007) underlines the urgent need to complete an ongoing modern taxonomic assessment of the family Tayassuidae. A revision of the peccaries is imperative to orient conservation management and planning as well as to increase understanding of the basic biology, ecology and evolution of this group (Taber 1993).

Differentiation within *P. tajacu*. Highly relevant to the claim by van Roosmalen et al. for a fourth species in the genus *Pecari* is that previous phylogenetic mitochondrial DNA studies have shown genetic variation within Colared peccary to be higher than that observed between *C. wagneri* and *T. pecari*, and was also higher than that observed between recognised species of the family Suidae (Gongora & Moran 2005; Gongora et al. 2006). Phenotypic, morphological, chromosomal and DNA data have been used to assess the levels of differentiation within *P. tajacu*. This lineage has a broad distribution in the sub-tropical and tropical ecosystems of the Americas comprising a wide variety of environments (rainforest, semi-arid thorn forest, coastal forest, cloud forest, deserts, islands, rangelands, scrublands, savannas, and freshwater wetland) between the south-western United States of America and northern Argentina (Grubb & Groves 1993). Its ancestry also seems to have an early divergence from the other peccary lineages in the Americas (Gongora et al. 2006). Early morphological studies provided the first evidence of cranial and dental variation between *P. tajacu* from throughout the Americas (Kiltie 1985; Woodburne 1968), although specimens were ultimately grouped into a single species. Variations in size and pelage colour, coupled with distribution data, have been the basis for proposing the existence of 14 subspecies of *P. tajacu* (Grubb & Groves 1993; Hall 1981). However, the inheritance of these traits has not been tested or substantiated by other methods.

Conventional cytogenetic (Builes et al. 2004; Gongora et al. 2000; Vasart et al. 1994) and cross-species chromosome painting (Adega et al. 2006; Bosma et al. 2004) studies showed variation in the structure of two chromosomes between *P. tajacu* specimens from Arizona, Colombia and Brazil, providing additional evidence for differentiation within this species. A single captive specimen from Colombia, heterozygous for a balanced translocation may represent a hybrid between the two different *P. tajacu* lineages (Builes et al. 2004). This may contrast with other cytogenetic studies (Adega et al. 2006) which propose a 'significant barrier' for hybridization between major Colared peccary lineages/species. However, germ line cytogenetic and/or reproductive studies are required to assess whether this possible hybrid is fertile before any conclusion can be addressed.

In this paper we revisit the genetic data from *P. maximus* (van Roosmalen et al. 2007) using a DNA dataset of the three peccary species generated by Gongora et al. (2005, 2006) and including 50 new DNA *P. tajacu* sequences from United States, Mexico, Colombia and Brazil. We also analyse the morphological and ecological evidence used to support the species status of *P. maximus* in the light of available literature.

MATERIAL AND METHODS

Sampling and DNA extraction. Blood, tissue and hair samples from 50 captive and wild *P. tajacu* from south-eastern and central-western Brazil (BRA1–BRA5; $n=5$); southern and northern Colombia (COL11–COL40; $n=30$); central and southern-central Mexico (MEX41–MEX48; $n=8$); and Texas in the United States (USA6–USA12; $n=7$) were used in this study (Appendix 1). DNA was extracted using either a standard proteinase K and phenol-chloroform protocol (Sambrook et al. 1989) or QIAamp DNA mini kits (Qiagen Pty Ltd).

PCR and Sequencing. We used previously published primers to amplify approximately 1,200 bp of the complete mitochondrial control region (Kim et al. 2002) at the University of Sydney, Australia. PCR was carried out using methods outlined in Gongora et al. (2005; 2006) except for sequencing of forward and reverse strands which were directly sequenced rather than clone inserts. Control region sequences (450 bp) from the Texan specimens ($n=7$) were independently generated at Purdue University. Primers, PCR and sequencing conditions were performed as described in Cooper et al. (2010). Although there is a difference in length between the above subsets of sequences, the corresponding regions are informative for assessing the major clades of *P. tajacu* described in previous studies (Gongora et al. 2006).

Data analysis. Forward and reverse sequences were overlapped in order to obtain a single double-stranded sequence for each animal using CodonCode Aligner v3.5.5 (CodonCode Corporation). After excluding flanking primer regions, the novel sequences (~1,120 bp, GenBank accession numbers HM102371 through HM102419) were aligned using the program Muscle (version 3.6; Edgar, 2004) along with those *P. tajacu* sequences (AY546539–AY546569) published by Gongora et al. (2005; 2006) and the single sequence (DQ009006) from *P. maximus* published by van Roosmalen et al. (2007). The control region from *T. pecari* (AY546516–AY546519) and *C. wagneri* (AY546520, AY546521) were included as an outgroup. The alignment used for analyses described consisted of 1,140 bp after excluding the tandem repeat motifs, except for a single motif, due to heteroplasmy according to Gongora et al. (2006). Because few gaps were observed they were kept in the alignment.

A separate dataset of concatenated nuclear PRE-1 642 and PRE-1 27 sequences was generated and aligned as described above. It consisted of available sequences from GenBank (*P. maximus*, DQ016372 and DQ016371; *P. tajacu*, DQ190931–DQ190883, AY569340–AY569339, and AY568052–AY568047; *T. pecari*, AY546331 and AY546528; and *C. wagneri*, AY546530 and AY546527).

The best fit DNA substitution model for the control region and PRE-1 alignments were selected by the program Modelgenerator (version 0.85; Keane et al. 2006) and implemented in Maximum Likelihood (ML) to reconstruct a phylogenetic tree using the software PhyML (version 3.0; Guindon & Gascuel 2003). The tree topology space was searched by using the best of Nearest Neighbour Interchange and Subtree Pruning and Regrafting starting from five random starting trees generated by BioNJ (Guindon & Gascuel 2003; Guindon et al. 2010). Branch support was calculated using the approximate likelihood ratio test (aLRT) with SH-like interpretation, as it is as conservative and accurate test compared with bootstrapping but less computationally intensive (Anisimova & Gascuel 2006; Guindon et al. 2010).

RESULTS AND DISCUSSION

Clustering of *P. maximus* within recognised major clades of *P. tajacu*. Novel and published Collared peccary mitochondrial control region sequences representing 44 haplotypes clustered in two major clades: North/Central American clade and South American clade (Fig. 1) as described by Gongora et al. (2006). The novel *P. tajacu* sequences from Brazil clustered within the South American clade closely related to two sequences from Argentina, while those from Texas clustered within the North/Central American clade closely related to specimens from Arizona, Mexico and Colombia. Sequences from Colombian specimens split between the two major clades consistent with previous studies of being a paraphyletic group (Gongora et al. 2006). The current results corroborate that the Gongora et al. (2006) dataset is suitable for assessing major subcontinental geographical origins of captive and wild specimens.

Unexpectedly for a sequence from what is considered as a different species, *Pecari maximus* clustered within the major South American clade closely related to central-western Brazilian and northern Argentinean sequences supported by high aLRT values (Fig. 1) rather than in a separate new clade. Consistent with control region analyses, ML tree of PRE-1 sequences shows that those from *P. maximus* cluster within the *P. tajacu* closely related to sequences from Bolivia, Colombia and the United States (data not shown). The clustering of *Pecari maximus* within a previously recognized South American clade of *P. tajacu* (Gongora et al. 2006) do not support the new species status of those specimens studied by van Roosmalen et al. (2007). Although there is no agreement as to which particular sequences accurately and universally reflect the species' boundaries (Vogler & Monaghan 2007), other molecular markers, such as cytochrome *b* or cytochrome *c* oxidase *I* are usually recommended as being more inform-

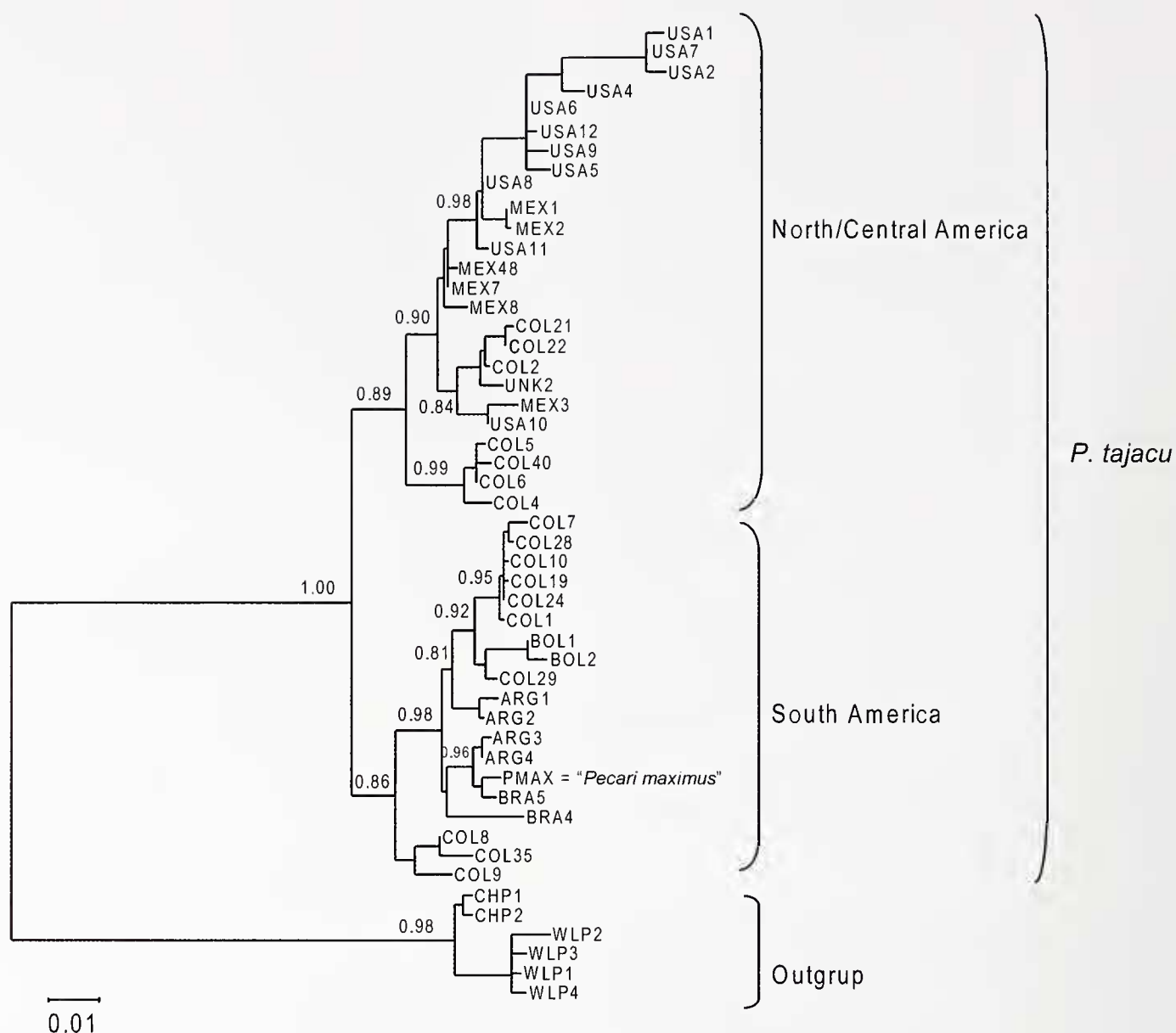


Fig. 1. Maximum Likelihood tree of the mitochondrial control region sequence representing forty-four haplotypes observed in eighty *P. tajacu* specimens, using both *C. wagneri* (CHP) and *T. pecari* (WLP) sequences as outgroups. Brackets indicate the two major clades found in *P. tajacu* with Colombian (COL) specimens showing paraphyletic relationships. *Pecari maximus* clustered within *P. tajacu* closely related to those specimens from Brazil (BRA) and Argentina (ARG). Details of samples used in this study are described in Appendix 1. Numbers close to branches are aLRT values. For clarity, only aLRT values for the main internal groups higher than 0.80 are shown.

ative to assess genetic species distinction (Blaxter 2004; Blaxter et al. 2005; Bradley & Baker 2001). Phylogenetic conclusions based on a single specimen are insufficient and uncertain. Under the current DNA evidence it is likely that single specimens studied by van Roosmalen et al. (2007) correspond to one of the *P. tajacu* lineages identified by Gongora et al. (2006). Species status has come and gone for some putative taxa within the distantly related suid family. For instance, the possible extinct *S. buc-*

culentus (Indochinese or Vietnam Warty pig) was initially considered as a separate species within the genus *Sus* (Groves 1997), but after DNA analyses showed that its sequences clustered closely with *S. scrofa* (domestic pig and wild boar), it has been suggested that it could correspond to a geographically restricted variant of *S. scrofa* rather than a distinct species (Mona et al. 2007; Robins et al. 2006).

Comments on the morphological, behavioural and ecological evidence of *P. maximus*. The body weights reported for *P. maximus* (van Roosmalen et al. 2007) are within the range reported for *P. tajacu*, albeit at the large end. For instance, Sowls (1997) reports exceptional weights of wild Collared peccaries in Arizona in excess of 42 kg, and Bodmer (1989) reports weights close to 40 kg in Peru. Bodmer et al. (pers. obs.) have observed considerable variation in the skull sizes of both *P. tajacu* and *T. pecari* from the Tahuayo, Yavari and Tamshiyacu regions of north-eastern Peru, well within the range reported by van Roosmalen et al. (2007). These preliminary observations are based on the collection held at the zoology museum of the Universidad Nacional de la Amazonía Peruana (UNAP), which consists of several thousand skulls collected by local subsistence hunters over a 10 year period. In addition, Bodmer et al. (pers. obs.) have recorded body weights from both *P. tajacu* and *T. pecari* hunted by local people in the Yavari river valley. Again, there is considerable variation, and the body weights are well within the range reported by van Roosmalen (Bodmer pers. obs.). Comparing *T. pecari* with the proposed new species, the former may similarly reach head-body lengths over 120 cm and weights as high as 40 kg in the Brazilian Pantanal (Keuroghlian et al. 2006) and 50 kg in the northern Amazon (Fragoso 1998). It would be desirable that skull measurements of the proposed *P. maximus* be statistically compared with those from extremely large *P. tajacu* found elsewhere in their range. Further, using skin pelage characteristics to distinguish species can be problematic since bristle colour may differ substantially within peccary species even in the same area (Gongora et al. 2006). In Collared peccaries, their lighter-haired collar pattern may vary from distinct in some individuals to barely noticeable in others. The most compelling morphological lines of evidence presented by van Roosmalen et al. (2007) are three photographs from three individuals of exceptionally long-legged peccaries which appear different from peccaries we are familiar with, but these are not backed up by measurements.

Ecological and behavioural differences have also been used to characterize peccary species (Sowls 1997). van Roosmalen et al. (2007) have attributed a number of differentiating traits for their peccary in line with this reasoning. However these claims are not based on intensive field observations, nor do they draw on recent literature concerning the ecology and behaviour of both *P. tajacu* and *T. pecari* to inform contrasts. For instance, while they claim that the new peccary uniquely lives in adult pair groups, sometimes with young, *P. tajacu* is also known to forage alone or in small groups, even while belonging to herds typically of six to twelve individuals (Keuroghlian et al. 2004; Sowls 1997; Taber et al. 1994), although larger groups have been reported from the Amazon (Fragoso 1994). Furthermore, the number of individuals

seen together may depend on the time of day. Radio telemetry studies have shown that *T. pecari* has distinct seasonal movements that are related to habitat and fruit availability within their large home ranges, and *P. tajacu* has relatively small stable home ranges (Altrichter et al. 2001; Fragoso 1998; Keuroghlian et al. 2004; Keuroghlian & Eaton 2008; Sowls 1997). Neither species can be described as roaming semi-nomadically as van Roosmalen et al. (2007) has suggested. Instead they commonly forage on freshly fallen fruits (Altrichter et al. 2000, 2001; Beck 2005; Keuroghlian & Eaton 2008). Therefore, these are not unique behaviours of *P. maximus*. Whether peccaries need to dig with their noses during foraging depends on the type of habitat where fruits are available, i.e. buried within the sediments of a swamp or exposed on the forest floor (Keuroghlian & Eaton 2008). With only three skulls attributed to the new species, sample size is too low to comment on tooth wear patterns. Also, the lack of scent from the new peccary skins may be related to the skill of the hunters (that remove scent glands during butchering; Keuroghlian pers. obs.). We note that subjectively there seems to be a considerable range between species and individuals with Chacoan peccaries having the least intense scent which may contribute to them being harder for the dogs of local hunters to track (Taber et al. 1993). Finally, observations are too limited, and overly dependent on local hunter hearsay, to draw conclusions that this possible new species has abandoned social groupings, group defence and territorial scent marking.

The possible discovery of a new peccary species from the Amazon basin is very exciting, and plausible, considering recent discoveries of new mammal species in this region mainly by van Roosmalen et al. (1998, 2000, 2002, 2003). However, based on the scant information reported by van Roosmalen et al. (2007), and the results of our own genetic analysis, we conclude that there is not enough evidence to support the claim of a new species, and that the specimens studied by van Roosmalen are most likely *P. tajacu*. We also consider that further DNA, cytogenetic and morphological research is necessary to better understand peccary taxonomy. Additional studies using other genetic molecular markers, cytogenetic, and morphological analyses incorporating new samples from all across the Amazon basin, will provide the basic information for understanding the genetic and morphology variation under the extant recognized species.

Acknowledgements. This study was funded by the University of Sydney International Program Development Fund to J. Gongora to support collaboration between the University of Sydney (Australia) and the Universidade de São Paulo (Brazil). Brazilian peccary samples were sourced under permit IBAMA 13601 from Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis and imported into Australia under permits AQIS IP07011173 and CITES, 09BR002827/DF. Other pec-

cary samples were sourced from wild and captive specimens collected for other studies from J. Gongora and J.D. Cooper. We thank Peter Waser and J. Andrew DeWoody for their support to J.D. Cooper to access the Collared peccary sequences from Texas. We also would like to thank all the institutions that collaborated in obtaining samples listed in Appendix I.

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Appendix I.

Origin of Collared peccary samples

Argentina: North, Ciudad de Rio Cuarto ARG1–2; Olavaria, ARG3–4; **Bolivia:** North, La Paz, Mallasa Zoo, BOL1–2. **Brazil:** State of Amazonas, PMAX; South East, State of São Paulo, BRA1–4; Central West, State of Mato Grosso do Sul, BRA5. **Colombia:** Central, Santa Cruz Zoo, COL1; Jaime Duque Zoo, COL2; North Central, Matcaña Zoo, COL4, COL20–22; Santa Fe Zoo, COL5; North West, Barranquilla Zoo, COL6, COL30–40; South Central, La Lagartija Zoo, COL7; La Lagartija Zoo, COL8; Cali Zoo, COL9; South East, Macagual Farm, COL10, COL23–29; Central, Santa Cruz Zoo, COL11–19; **Mexico:** Central, Guadalajara Zoo, MEX1–2; North, Puebla Zoo, MEX3–4, MEX41–42; South Central, Mexico DF Zoo, MEX5–8, MEX43–48. **USA:** Arizona, USA1–3; Texas, USA4–12. **Unknown:** Adelaide Zoo, UNK1–2.

Received: 23.10.2010

Accepted: 25.01.2011

Corresponding editor: R. Hutterer